STAND STRUCTURE IN A KAMAHI (*WEINMANNIA RACEMOSA*) FOREST AT WAIMANGAROA, BULLER COUNTY

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ABSTRACT

A coastal temperate rainforest dominated by *Weinmannia racemosa* was sampled by two belt transects totalling 0.2 ha in area. Reproduction of all woody species is almost entirely by seed. The population of *Weinmannia racemosa* consists mostly of mature individuals which form most of the canopy from which large scattered specimens of *Metrosideros robusta* emerge. The few young plants of *W. racemosa* are usually found as epiphytes on tree ferns, *Dicksonia squarrosa*. The subcanopy trees, particularly *Myrsine salicina* and *Hedycarya arborea* are regenerating well and have balanced all-aged structures. Podocarps are sparsely distributed through the forest except at the margin. Regeneration is poor but probably sufficient to maintain the present density. Regeneration of podocarps is suppressed in the virgin forest at present but this may only be a stage in the cycle of forest growth.

INTRODUCTION

This study was carried out in May 1976 by members of the Third Year Plant Ecology class. An area of coastal temperate rainforest was sampled and the height and diameter classes of all trees greater than 3 m tall were measured. Hypotheses to explain the observed population structures of the tree species are advanced.

The members of the class were Linda Budgeon, Kevin Hackwell, Les Hitchcock, Lim Siow Sheong, Ian Lineham, Graham McDonald, David Nimmo, Bronwyn Welch and Rob Young.

In August 1976, Dr L. Kucera and Dr A.T. Dobson revisited the site and took levelling measurements.

THE STUDY SITE

The study site is situated on the coast at Waimangaroa about 12 km north-east of the town of Westport (NZMS 1 S24/213785 or c. 41°43'S, 171°44'E). The coastal plain in this area is now farmed with some forest remnants. The remaining forests are in private ownership and are being converted to farmland. These forests do not have any value for timber. This study was carried out near the northern margin of the most extensive area of forest remaining on the coastal plain.

The soils have formed on dune sands of recent origin being no more than 6500 years old and perhaps much younger (Nathan, 1976). Harris and Harris (1939) place the soil in the Utopia series and describe it as a sandy loam with a slight development of podsolisation. A very thin iron pan commonly occurs in the B horizon. Harris and Harris (1939) state that most of the nutrients have been lost from the Utopia soils through leaching. However, the luxuriance of the forest compared with others in the region, the leaf litter which, although acid (pH 3.6-4.6), is between mull and mor in type, the presence of earthworms, and the good pasture which may be obtained after the land is cleared all suggest reasonable levels of fertility. Nutrients from sea spray help to maintain fertility against leaching losses.

The climate is mild and humid. Data supplied by the New Zealand Meteorological Service from Westport Aerodrome for the period 1944-1970 give a mean rainfall of 2159 mm evenly distributed through the year and falling on 193 days. Average relative humidity is 80% at 9.00 a.m. throughout the year except for the month of June when the atmosphere is drier (59%). Potential evaporation (Thornthwaite average) is 639 mm per year, the remaining precipitation becoming run off. On average a water deficit is recorded on only one day per year. Snow averages less than one day per year but ground frosts occur on 44 occasions each year and screen frosts once a year. The severest ground frost on record is -7.7°C. Mean annual temperature (1937-1970) is 11.9°C, mean daily maximum 15.7°C and minimum 8.5°C. Sunshine hours (1937-1970) are high with a mean value of 1941 hours being recorded (45% of possible). As a percentage of possible, sunshine hours are evenly distributed over the year. The main winds and also the strongest are from the south-west and west (Furkert 1947) with north-easterlies and easterlies being common but less frequent.

The coastline at Waimangaroa consists of low sandy cliffs 2-4 metres tall. The ocean currents and prevailing south-westerly winds result in long-shore drift of material along the coast in a north-easterly direction. However, the construction of moles at the mouth of the Buller River has stopped the movement of material. Subsequently there has been severe erosion of the coast north-east of Westport. Furkert (1947) estimated that the rates of erosion between 1890-1905 averaged about 8 metres a year but had dropped to about 2.5 metres a year between 1921-45. However, erosion still continues and may even have increased slightly in recent years. The combination of coastal erosion and clearing of the land may eliminate this forest entirely in a few years.

The forest shows little sign of disturbance except at the margins. Cattle have grazed the margins in the past although the density of supplejack (*Ripogonum*) vines and other shrubs has deterred them from penetrating more than 10 metres. The forest margin adjacent to the study area is now fenced, and there has been some spraying of gorse along the fence line but this has not affected the forest interior. Opossums occur in the forest but do not cause obvious damage. The forest is damaged by salt spray and wind for about 30 metres from the coast and there are many dead canopy trees in this zone. The terrain is gently undulating with up to two metres variation in height.

METHODS

The study site was selected arbitrarily and ran perpendicular to the coastline about 80 metres from the sea shore at its nearest end. It was no nearer than 50 metres to the fenced pasture at any point.

A line 100 metres long was laid down through the forest and two parallel lines were laid 10 metres either side of the principal line. The two belt transects so formed were sampled separately. The students were divided into groups of two or three. Each group worked systematically along the transects and between them all trees and tree ferns greater than 3 metres tall were sampled. The position of each individual tree along the transect was recorded. Canopy height (using abney levels) and diameter at breast height were measured. Notes were made on the epiphytic and vine flora of each individual and on other species present in the plot. A few increment cones were taken for ageing. One of the transects was levelled using standard surveying equipment. The levelling results have not been shown but there was no apparent relationship between topography and vegetation.

The relatively small size of the plot (0.2 ha) is likely to be the main source of error. However, a general inspection of the surrounding forest did not suggest that this site was unrepresentative of the surrounding forest.

RESULTS

THE CANOPY AND SUBCANOPY FOREST STRUCTURE

The spatial relationships between the tree species and tree ferns greater than 3 metres tall are presented schematically in Figure 1. Diameter size classes of the principal species are given in Figure 2. Table 1 lists the basal areas for all species with individuals in the canopy or subcanopy and also lists all species present with notes on their abundance.

The dominant species in the forest is *Weinmannia racemosa* (Kamahi) which accounts for over 80% of the total basal area. The main canopy tree, most individuals are 15-20 metres tall with occasional specimens up to 25 metres. Rising above the general canopy are occasional individuals of *Metrosideros robusta* (rata) and although few in number they are conspicuous when the forest is viewed from a distance. Occasionally contributing to the canopy and scattered throughout the forest are three podocarp species. *Podocarpus dacrydioides* (kahikatea) is the most common whereas *Dacrydium cupressinum* (rimu) and *Podocarpus ferrugineus* (miro) are very scattered. Near the study site a single specimen of *Elaeocarpus dentatus* (hinau) contributed to the canopy.

Except for the podocarps, few of the canopy trees are straight-trunked. *Weinmannia racemosa* individuals are often branched low-down and many specimens are leaning, occasionally strongly so. The schematic representation of the transects

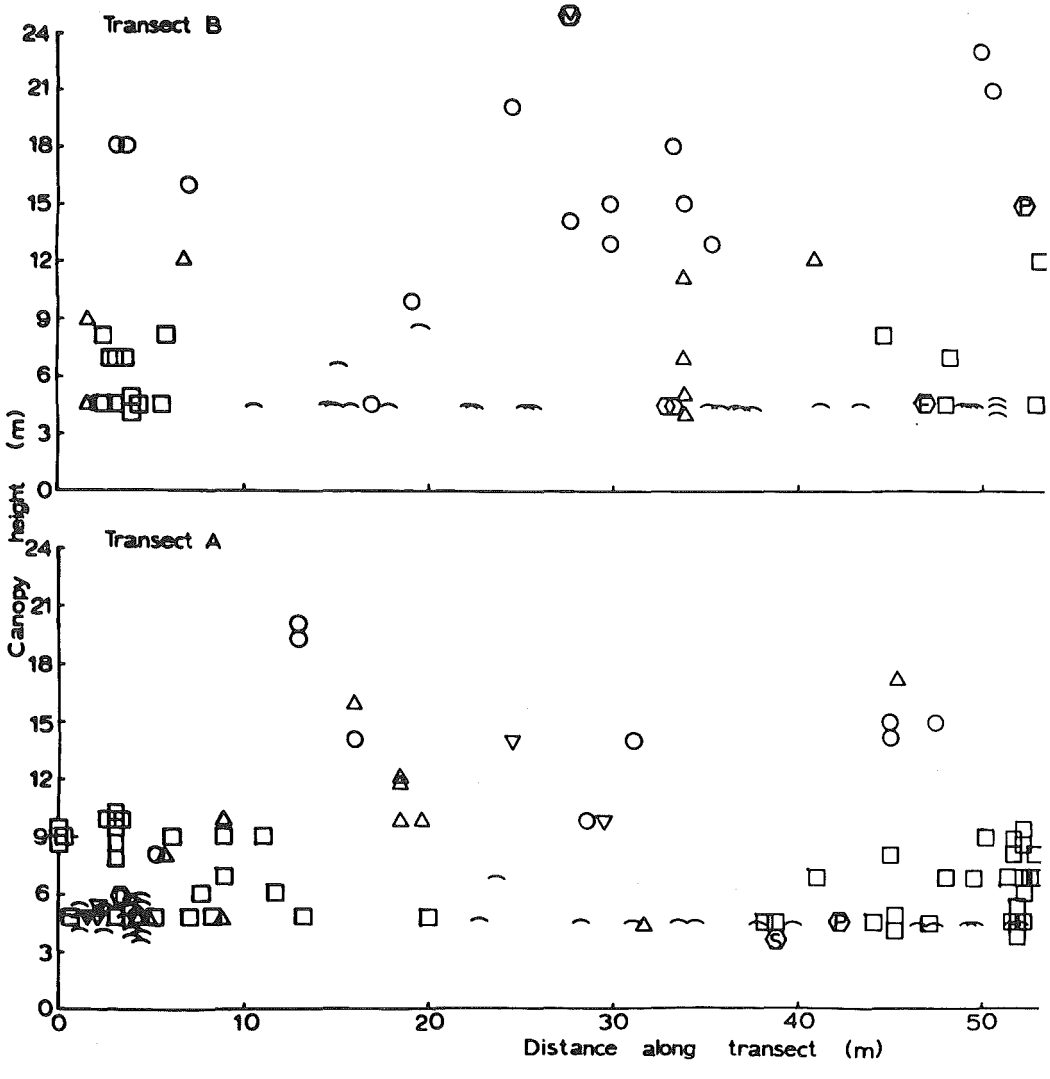


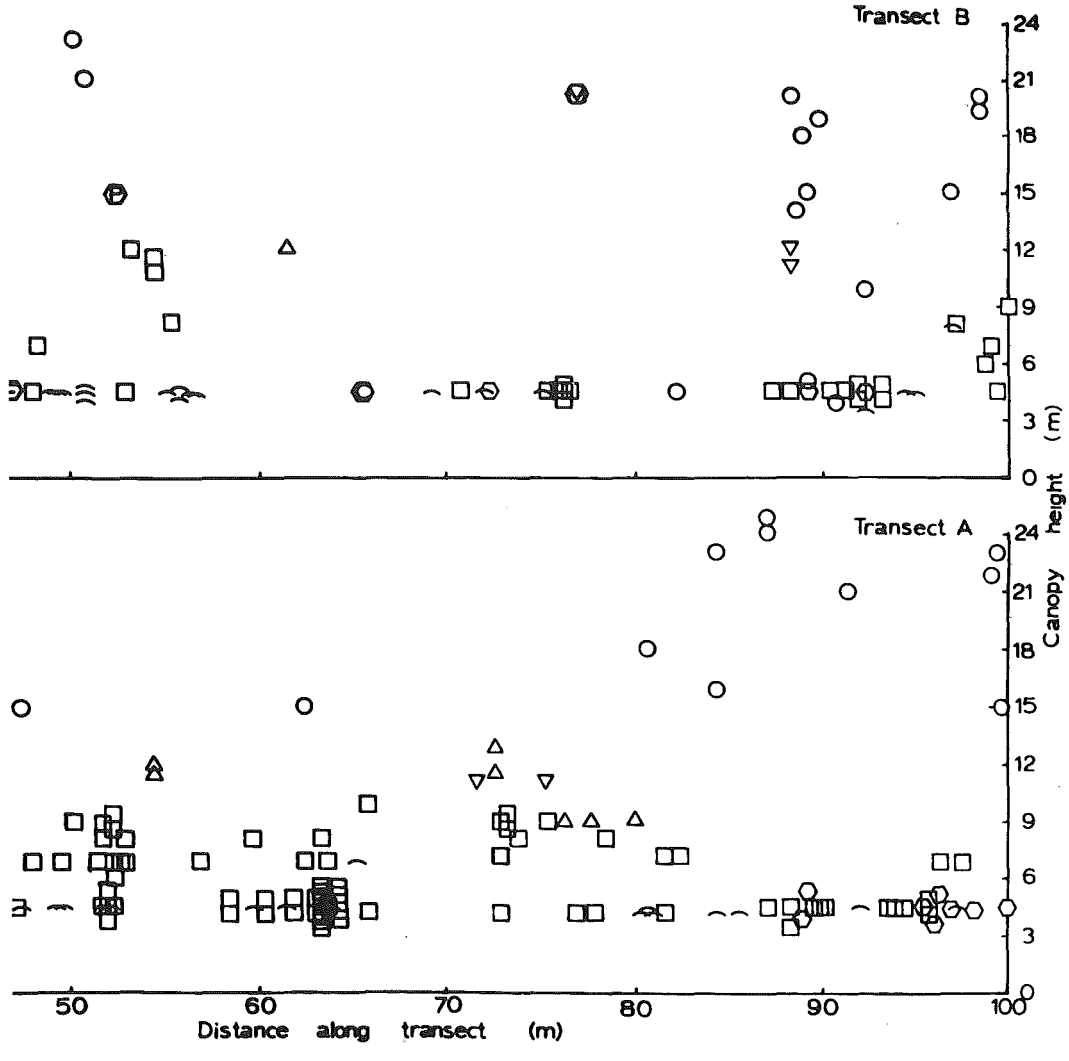
Fig. 1. The distribution of individual trees greater than 3 m tall in two contiguous, parallel transects in rainforest at Waimangaroa, showing position of individual along transect and its canopy height.

Weinmannia racemosa

Hedycarya arborea

Myrsine salicina

Melicytus ramiflorus



Dicksonia squarrosa

Pseudowintera axillaris

C *Coprosma australis*

D *Dacrydium cupressinum*

F *Podocarpus ferrugineus*

M *Metrosideros robusta*

P *Podocarpus dacrydioides*

S *Schefflera digitata*

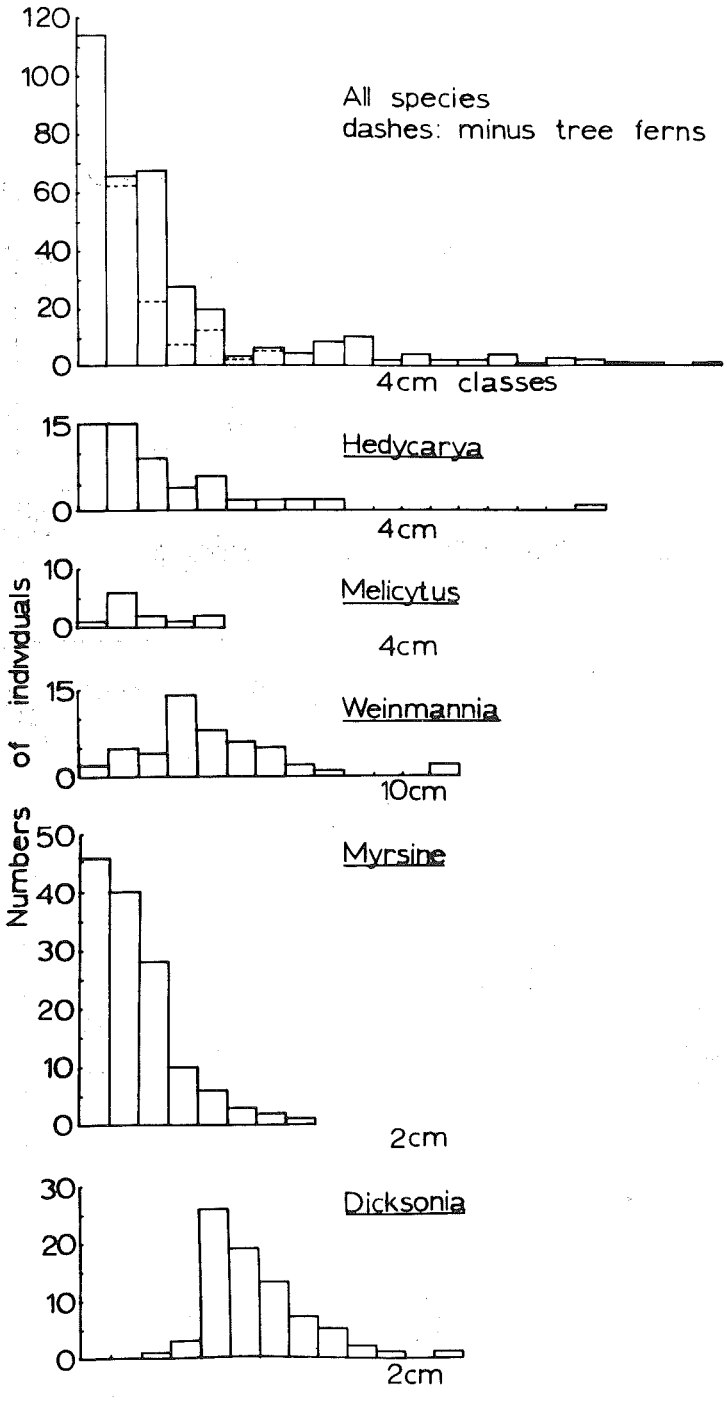


Fig. 2. Diameter size classes of the principal species in the transects in rainforest at Waimangaroa.

TABLE 1. SPECIES PRESENT IN WAIMANGAROA FOREST PLOT.

(a) Woody species over 3 m tall and their basal areas

	dm^2/ha
Weinmannia racemosa	6158.60
Hedycarya arborea	669.90
Metrosideros robusta	616.40
Dicksonia squarrosa	529.40
Myrsine salicina	204.00
Melicytus ramiflorus	58.75
Podocarpus dacrydioides	45.40
Pseudowintera axillaris	14.35
Coprosma australis	2.50
Podocarpus ferrugineus	1.40
Dacrydium cupressinum	0.65
Schefflera digitata	0.65
TOTAL	7638.80

(b) Other woody species

Aristotelia serrata	rare
Carpodetus serratus	frequent
Coprosma areolata	common
C. foetidissima	frequent
C. rotundifolia	common
(*C. propinqua*	just outside plot, rare)
Elaeocarpus dentatus	rare, large canopy tree outside plot
E. hookerianus	rare
Fuchsia excorticata	rare
Griselinia lucida	common, epiphyte
(*G. littoralis*	small tree outside plot)
Pseudopanax colensoi	rare
P. crassifolius	rare
P. edgerleyi	rare
Streblus heterophyllus var. *heterophylla*	common

(c) Dictoledonous herbs

Nertera dichondraefolia	rare, ground cover

(d) Monocotyledonous herbs

Collospermum hastatum	common, epiphyte
Earina mucronata	epiphyte
Microlaena avenacea	frequent
Uncinia unciniata	common

(e) Lianes

Freycinetia bauriana	common
Metrosideros diffusa	common
M. fulgens	common
M. perforata	common
Parsonsia sp.	rare
Ripogonum scandens	common 128 stems/0.01 ha
Rubus australis	rare

(f) Ferns

Asplenium bulbiferum	common
A. falcatum	frequent, epiphyte
A. flaccidum	frequent, epiphyte
Blechnum chambersii	frequent
B. discolor	rare
B. "procerum"	rare
Granitis billardieri	rare, low epiphyte
G. ciliata	rare, low epiphyte
G. magellanica ssp. *nothofageti*	rare, low epiphyte
Histiopteris incisa	rare
Hymenophyllum dilatatum	frequent, epiphyte
H. revolutum	frequent, epiphyte
H. sanguineolentum	frequent, epiphyte
H. scabrum	frequent, epiphyte
Lastreopsis hispida	common
Leptopteris hymenophylloides	frequent
Phymatosorus diversifolius	rare, epiphyte
P. scandens	common, epiphyte
Rumohra adiantiformis	rare
Trichomanes reniforme	rare, epiphyte
T. venosum	rare, epiphyte on tree fern

(Fig. 1) is therefore somewhat misleading. Many of the apparent gaps are overhung by leaning trees. However, a few gaps, such as the one between 55-65 m along Transect B, are due to recently fallen trees. In Transect A the gap of 24 m is due to the presence of an intermittently waterlogged depression. Not all such depressions are liable to waterlogging.

A subcanopy is formed by *Myrsine salicina* (toro), *Hedycarya arborea* (pigeonwood), *Melicytus ramiflorus* (whiteywood), *Weinmannia racemosa* and the tree fern, *Dicksonia squarrosa*. There are small numbers of other species. Although not contributing greatly to the forest in terms of basal area, *Myrsine salicina* is the most numerous tree in the forest but most individuals are seedlings, saplings and poles. There are few specimens of even moderate girth. *Hedycarya* is well-represented in the subcanopy and like *Myrsine* the size class distribution has the typical J-shaped curve for balanced all-aged populations. Both moderately girthed and one large specimen of *Hedycarya* are present. The trees are well distributed. *Melicytus ramiflorus* trees are few in number but scattered throughout. Similarly subcanopy specimens of *Weinmannia* are few in number and the distribution of size classes demonstrates the lack of replacement of this species (Fig. 2). *Dicksonia squarrosa* is numerous but distribution of individual trunks is local and gregarious. Either conditions are not suitable for this fern in all parts of the forest or vegetative reproduction is the cause of the non-randomness. The lack of smaller diameter classes is due to the mode of growth of tree ferns. *Pseudowintera axillaris* is scattered locally as pole specimens to 5 m tall and occurs in shadier situations with little other shrub or small tree vegetation.

LIANES AND EPIPHYTES

The two life forms are both conspicuous features of the forest vegetation at Waimangaroa. It is virtually impossible to assess either quantitatively with the exception of *Ripogonum scandens* (supplejack).

Within a 10 x 10 m (0.01 ha) quadrat randomly selected from within the transects 128 stems of *Ripogonum* were counted. *Ripogonum* stems often arise from well-defined rootstocks which are spaced between the trees. Stems arising from the rootstock often remain unbranched until reaching the canopy and so are easily counted. All the remaining lianes sprawl and branch on the ground and as they climb. *Metrosideros diffusa, M. perforata, M. fulgens* (rata vines) and *Freycinetia bauriana* (kiekie) are abundant. All four are rootlet climbers. *Parsonia* and *Rubus* are rare.

Metrosideros species are abundant on all but young, smooth-barked saplings. *Freycinetia* is virtually confined to the larger canopy trees as are the woody epiphytes and the robust clumps of *Collospermum hastatum*. Of the woody epiphytes, *Griselinia lucida* is confined to this habitat and is often a component of the canopy. The other woody plants occurring as epiphytes are either shrubs which were also part of the terrestrial shrub layer, especially *Coprosma australis*, or young plants of the canopy and subcanopy trees. Both groups tend to be restricted to the lower trunks where transpiration rates are presumably lower and there is a greater depth of organic matter in which to root. *Collospermum* is a middle to high epiphyte not usually occurring below 3 metres.

Seedlings of *Weinmannia racemosa* are frequent only on the trunks of tree ferns. Whether as epiphytes on other species or ground-dwelling they are otherwise rare. Wardle (1966) stated that *Dicksonia squarosa* is the principle habitat in which *W. racemosa* establishes in virgin rainforest.

Among the herbs the principal low epiphytes are ferns. Of the filmy ferns (*Hymenophyllum* and *Trichomanes*) *H. dilatum, H. scabrum* and *H. sanguineolentum* are common and often occur mixed together. *Phymatosorus scandens, Asplenium flaccidum* and *A. falcatum* are frequent. The remaining epiphytic ferns are all uncommon or rare. The only high epiphyte observed was *Earina mucronata*.

SHRUB AND GROUND VEGETATION

The woody plants below 3 m tall are not evenly distributed as most species have a preference for the better illuminated areas. Several species of small-leaved, twiggy shrubs are prominent in the shrub layer particularly *Coprosma rotundifolia, C. areolata, Carpodetus serratus*, and juvenile, but no adult, *Streblus heterophyllus* and *heterophylla*. Common broad-leaved shrubs are *Coprosma australis, Schefflera digitata* and juvenile *Myrsine salicina*. *S. digitata* occurs most frequently in the damper hollows where water stands intermittently and it is seemingly more shade tolerant. The remaining shrubs are mostly juveniles of larger species which may or may not be represented in the

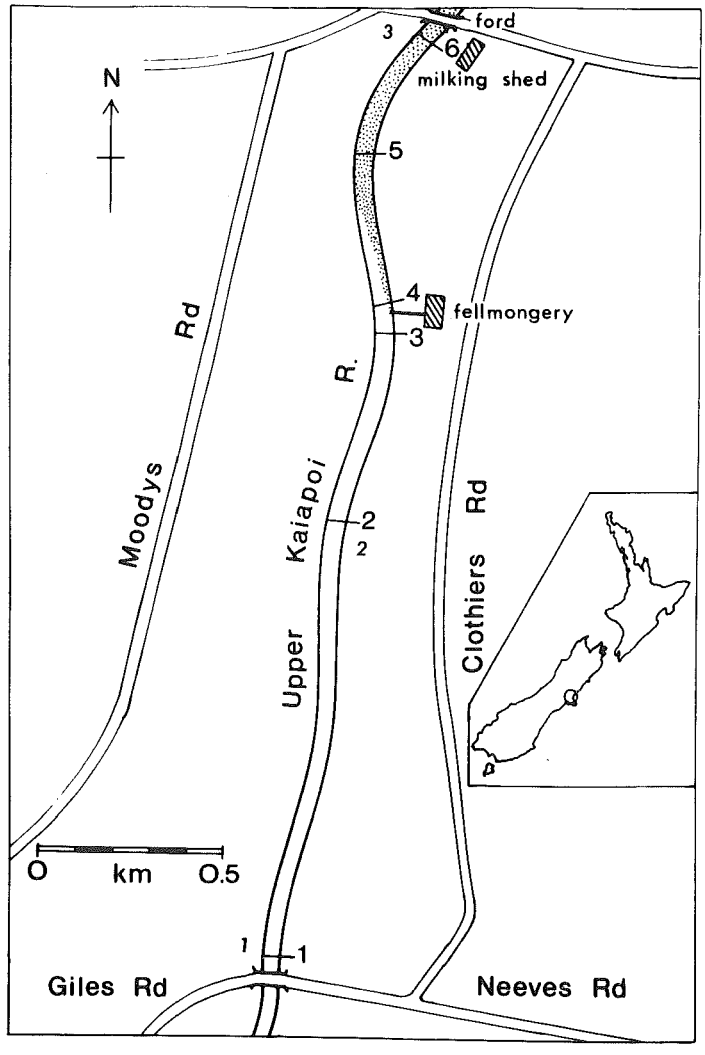


Fig. 1. Study area of the Upper Kaiapoi R. showing stations 1-6. Stippling indicates that part of the river polluted by fellmongery effluent. *1, 2, 3* show the stations described in Hirsch's study (1958). River and roads not to scale.

stations 3 and 4 from the east bank, and by station 5 was evenly dispersed across the stream. Some suspended solids from the effluent were deposited in the deep stretch between stations 5 and 6. Further organic wastes were discharged into the stream from a milking shed just above station 6.

The study was carried out during early winter (April, May, June 1971) when river temperatures ranged from 8.5°C to 13°C. River temperature was unaffected by the effluent discharge.

canopy. These juveniles are scattered throughout and the majority are suppressed. Where the canopy is less dense there may be opportunities for some of these suppressed species but these sites are usually filled with a vigorous growth of *Myrsine salicina, Streblus heterophyllus* and *Coprosma* species. Hence very few of these suppressed species seem likely to contribute to the next generation of canopy trees. The few individuals in favourable position are growing as low epiphytes or on decaying stumps.

The commonest podocarps in the shrub layer are those of *Podocarpus dacrydioides* which are most common in periodically flooded depressions. In this position they are invariably suppressed by overhanging branches. A few individuals are situated on better-illuminated hummocks and these are more vigorous. *Dacrydium cupressinum* saplings are rare but have a distinct preference for well-lit mounds and stumps so that despite their rarity these individuals have a chance of attaining the canopy.

The herbaceous vegetation is composed mostly of ferns and these have a preference for the better illuminated sites. The distribution of the herbaceous vegetation is discontinuous and nowhere is there complete ground cover. Even areas with more than 50% cover are very local. The common ferns are *Lastreopsis hispida, Asplenium bulbiferum, Blechnum chambersii* and *Leptopteris hymenophylloides*. The graminoids *Uncinia unciniata* (hook-grass) and *Microlaena avenacea* (bush rice grass) are scattered throughout.

GENERAL DISCUSSION

The size class distribution for trees shows the typical J-shaped curve for balanced all-aged populations (Fig. 2) and indicates that overall the forest is regenerating satisfactorily. However, the dominant species, *Weinmannia racemosa*, has a very uneven size distribution with very few young trees and saplings. The majority of the tree ferns have epiphytic seedlings on their trunks but the absence of saplings suggests that the seedlings may not be surviving for more than a few years. *Weinmannia* evidently is not replacing itself at the present time. The existing individuals are mostly mature specimens and the canopy is starting to open as they senesce and fall. *Weinmannia* is failing to regenerate from suckers or coppice shoots at Waimangaroa. Vegetative regeneration may be important in other forests where *W. racemosa* is abundant (Wardle 1966, Burrows *et al.* 1975). While it was not possible to obtain a complete core for dating, partial cores were obtained from several individuals. This indicated that there was a mean diameter increase of about 3 mm per year. As the most numerous size class is 0.3 m - 0.4 m, this suggests that these individuals are 100-130 years old. However, the two very large specimens may be 400 years old.

Most of the replacement is by subcanopy poles and saplings of *Myrsine salicina* and *Hedycarya arborea*, the former being numerically very abundant. Both have J-shaped size distribution curves. A 0.16 m diameter specimen of *M. salicina* was aged at c. 65 years and another at c. 50 years. Most of the

specimens of *M. salicina* are much smaller than this which suggests that the abundance of this species is a recent phenomenon. No ancient senescent specimens were observed. *Hedycarya* is less abundant but larger and probably older specimens occur than in *M. salicina*. Although these two species are not usually considered to be forest dominants, it seems that in the immediate future they will become more important as the *Weinmannia* canopy opens. Whether other species such as *Streblus heterophyllus* will enter the subcanopy is difficult to assess.

Metrosideros robusta seedlings normally begin as high epiphytes. The abundance of mature *Weinmannia* ought to provide an abundance of establishment sites but it is not possible to assess how much regeneration of *M. robusta* is occurring.

Regeneration of podocarp is only at low levels but as adult trees are also uncommon, regeneration is probably sufficient to maintain present density. Poor regeneration of the podocarps is due apparently to suppression by other species. At the margin of the forest where there has been disturbance, regeneration of the three podocarps is better, *Podocarpus dacrydioides* being especially numerous. Scattered through the farmland of the coastal plain are even-sized stands of podocarps, mostly *P. dacrydioides*. These are emerging from *Leptospermum* (manuka) scrub and fern which has arisen following the destruction of the original forest.

In considering podocarp regeneration in virgin forest at Pureora, central North Island, Beveridge (1973) maintained that a cyclic regeneration process occurs, although he is not the first to suggest such processes (see e.g Poole 1937). Beverdige describes the stages in the cycle as follows:

(1) Windfall of a large overmature podocarp.

(2) Invasion or increase of tree ferns until a colony of rhizomatous *Dicksonia squarrosa* is formed. The dense litter inhibits terrestrial recruitment of all podocarps and hardwoods.

(3) Development of epiphytic growth of hardwoods, particularly kamahi, on tree fern stems.

(4) Suppression and death of most of the tree ferns by hardwoods, and development of kamahi to a large size when it becomes a suitable perching tree for birds, particularly pigeons.

(5) Recruitment of podocarp seedlings mainly from bird-dispersed seed.

(6) Development of a podocarp sapling group as the kamahi crown thins and dies. Windfall of adjacent podocarps at this stage may enlarge the gap and hasten development of the podocarp group.

If such a cyclic process is operating at Waimangaroa then the cycle is largely at Stage 4. However, some thining is

occurring but with replacement of *Weinmannia* by other hardwoods. Whether hardwoods such as *Myrsine salicina* and *Hedycarya arborea* could dominate the forest for long is not known. There is no evidence that podocarps are replacing *Weinmannia* at Waimangaroa. It may be that regeneration of podocarps would be more vigorous under a canopy of *Myrsine* and *Hedycarya* and that the forest would then develop along a similar course to that described by Beveridge. More evidence is needed.

ACKNOWLEDGEMENTS

Mr J.F. Colligan of Waimangaroa kindly gave permission to work on his property. Climatic data were supplied by the New Zealand Meteorological Service.

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